74–8

Proceedings of the American Academy of Arts and Sciences

VOL. 74, NO. 8, P. 281–285—OCTOBER, 1941

PHOTOGRAPHIC EVIDENCE ON THE VISIBILITY OF COLOR PATTERNS IN BUTTERFLIES TO THE HUMAN AND INSECT EYE

BY CHARLES T. BRUES
Biological Laboratories, Harvard University

(Continued from page three of cover)

VOLUME 74

1. Bridgman, P. W.—The Measurement of Hydrostatic Pressure to 30,000 kg/cm². pp. 1–10. October, 1940. $0.35.
2. Bridgman, P. W.—The Linear Compression of Iron to 30,000 kg/cm². pp. 11–20. October, 1940. $0.35.
3. Bridgman, P. W.—The Compression of 46 Substances to 50,000 kg/cm². pp. 21–51. October, 1940. $1.00.
4. Bartlett, J. H. and Watson, R. E.—The Elastic Scattering of Fast Electrons by Heavy Elements. pp. 53–68. October, 1940. $0.65.
5. Brues, Charles T.—Fossil Parasitic Hymenoptera of the Family Scelionidae from Baltic Amber. pp. 69–90. October, 1940. $0.75.
6. Records of Meetings; Biographical Notices; Presidents of the Academy; Officers and Committees; List of Fellows and Foreign Honorary Members, etc.; pp. 91–192. November, 1940. $2.00.
7. Carpenter, F. M.—A Revision of the Nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae and Dilaridae (Neuroptera). pp. 193–278. December, 1940. $2.25.
8. Brues, Charles T.—Photographic Evidence on the Visibility of Color Patterns in Butterflies to the Human and Insect Eye. pp. 281–285. October, 1941. $0.35

Proceedings of the American Academy of Arts and Sciences

Vol. 74, No. 8, P. 281–285—October, 1941

PHOTOGRAPHIC EVIDENCE ON THE VISIBILITY OF COLOR PATTERNS IN BUTTERFLIES TO THE HUMAN AND INSECT EYE

By Charles T. Brues

Biological Laboratories, Harvard University

PHOTOGRAPHIC EVIDENCE ON THE VISIBILITY OF COLOR PATTERNS IN BUTTERFLIES TO THE HUMAN AND INSECT EYE

By Charles T. Brues

Biological Laboratories, Harvard University

Received December 12, 1940 Presented December 10, 1940

Aside from the plumage of birds, the most striking and conspicuous color patterns among animals are those found on the wings of butterflies. Some of these colors are due to pigments, others, particularly the metallic ones, are physical and the two types may occur in close combination.

We assume first that these color patterns are of recognition value to the butterflies themselves, and their development may have been influenced by sexual selection.

Furthermore they may represent something of a much more complicated nature. The independent discovery by Bates, Wallace and Trimen of remarkable resemblances in color pattern between various diverse butterflies made in the sixties of the past century is now well known to entomologists and biologists generally. The theories to explain these parallelisms on the basis of natural selection acting upon variations in palatable or mimicking species and tending to make these evolve into forms resembling unpalatable and "protected," but unrelated species, are equally common knowledge and have led to much controversy and a vast, detailed literature at the hands of later observers and theorists. Such disputation is still rife, and it must be admitted that no sane pronouncement may be made at the present time on the merits of the opposing views and I hold no brief for or against any of them. Nevertheless I am venturing to add a few notes on color vision among the insects themselves.

On account of certain inherent defects in human vision we see only a limited range of the spectrum and this does not coincide with the band that stimulates the eyes of certain other animals. Consequently we cannot hope to appreciate the color patterns of objects as seen for example by an insect without resorting to some subterfuge that enables us to shift our vision into the shorter wave lengths of light by blinding ourselves to the red and orange and at the same time penetrating into the invisible ultra-violet. Such possibilities are of course easily possible through certain simple photographic procedures. These were not available to the earlier students of mimicry, although they surmised that something might quite possibly be wrong with their interpretation of visual images in insect eyes.

Strangely enough, only scant attempts have been made in recent years to examine color patterns among butterflies by photography in light other than our own violet to red range of $\lambda 4000$–$\lambda 7600$. In 1933 Lutz published a number of photographs of butterflies registering the ultra-violet light reflected from their wings and gave an interesting account of the great change that takes place in the pattern of a number of species when thus illuminated, with our own entire range of vision excluded!

As nearly as has been ascertained the visual range of insects extends far into the ultra-violet, including wave lengths much shorter than those of sunlight after passage through the earth's atmosphere. Generally, however, it reaches only to about $\lambda 5900$ in the other direction and it is probable that the eye of most insects is not or only weakly receptive to colors which we see as orange and red. Such is undoubtedly the case with some types of insects and its extension to all is hardly open to much serious question, although we know that some species react slightly to orange and red and that they may confuse certain colors in the sense that they appear partially color blind. There is, of course, no close agreement between the numerous workers who have attempted to determine color sensitivity or perception among insects. As Lutz has clearly indicated (1933) the earlier experimenters failed to reckon with the ultra-violet, particularly in dealing with insects that visit flowers. Some other work has likewise been marred by failure to eliminate smell and memory. So far as the butterflies are concerned, Eltringham (1919) has brought much evidence forth to show that they distinguish colors fairly well except in the red

region in the case of some species. Some of his conclusions however are not necessarily sound as he omits consideration of ultra-violet.

On the other hand so far as the terrestrial vertebrate enemies of insects are concerned it appears from the researches of Hess and others that their vision does not depart radically from that of the normal human being, consequently their relation to the phenomenon of mimicry is not affected by the matters specifically dealt with here.

Before proceeding to a discussion of our results, attention should be drawn to some other matters relating to color and mimicry. The simpler cases of mimicry among butterflies relate only to a single species serving as the model and another acting as the mimic and the similarity between the two is a coincidence of the color pattern, in form and shade in the two species without reference to any other related or unrelated species. In the case of Müllerian mimicry as first noted by Fritz Müller where numerous individual examples of mimicry in a region occur together, involving a series of related models and a series of mimics, there is a marked tendency toward the appearance of certain similar color patterns among several pairs of species. Moreover, this type commonly involves yellow, orange and red patterns to which insects are apparently only slightly sensitive.

In the photographs which form the basis for the present contribution I have attempted to reproduce in monotone the visual image that each butterfly should produce in the eye of another butterfly or other insect. It is freely admitted that one makes a bold assumption to believe that these are close to accuracy, but they represent an approach in this direction and have revealed a possible discrimination of tone and brilliancy that were not anticipated at the outset of the experiment.

The butterflies selected are mainly the species illustrated in Punnett's "Mimicry in Butterflies" (1915) which include many of the more striking and better known cases that have been noted. This material was available in the large Week's collection of the Museum of Comparative Zoology, and I am very grateful for the opportunity to make use of the specimens from this collection for the present purpose.

All the photographs were made with a Leica camera fitted with focussing attachment, the exposures determined by trial and error. Those for ultra-violet light are short, but satisfactory exposures for fluorescence required, with our apparatus, about ten minutes each. Although the methods used are simple, much time is required for the necessary manipulations as well as the processing of the black and white negatives and positives. For a considerable part of this tedious work I am indebted to Mrs. A. S. O'Connor who aided me throughout the several operations.

Four photographs were made of each butterfly. A natural color transparency on Kodachrome film gives a very accurate picture of the color pattern as seen by the human eye. These exposures were made on Kodachrome A film illuminated by a pair of flood-light bulbs. For the three other photographs which are in monotone, a quartz mercury vapor lamp ("Uviarc") was used as the source of illumination, enclosed in a light-tight box provided with a window.[1] For two of the others this window was covered by a filter (Wratten No. 18) that transmits ultra-violet only, absorbing all the visible spectrum. Thus illuminated (Fig. 1, A) it is possible without further filters to secure a photograph of the ultra-violet as reflected by the wings, using an orthochromatic film that serves to eliminate a very slight amount of red that passes through the No. 18 filter.

Since there is much variation in the transparency of different photographic lenses to ultra-violet light, it is important to know the spectral limit passed by any particular lens before attempting to interpret photographs made with it. I am deeply indebted to Professor Theodore Lyman of Harvard University who had such determinations made for me in his laboratory. The Leitz "Elmar" lens was found to pass the band at $\lambda 3131$ and also, of course the one near $\lambda 3650$. On this account it was deemed suitable for our present purpose.

It is not possible to reproduce the color photographs here and the reader who may not be familiar with the species dealt with is referred to Punnett's book ('15) in which the colors are shown with close fidelity.

Some of the pigments on the wings fluoresce when illuminated by ultra-violet light and this pattern is visible to the human eye without any further filter since the fluorescent light is within our visual range. It varies greatly in different forms as might be expected, since there is a wide range in both color and intensity among all sorts

[1] Viewed directly in this light, without any filter, the colors and patterns of the butterflies appear to our own eyes essentially as they do in daylight.

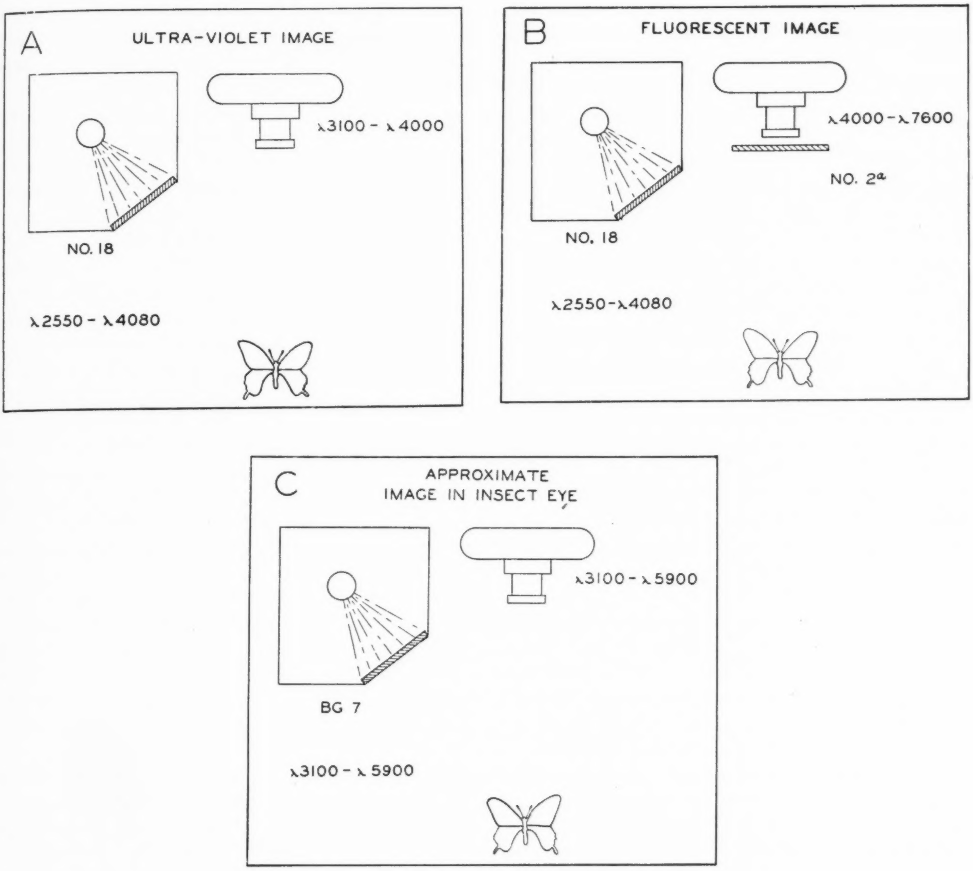


Fig. 1. Arrangement of light, filters and camera used in securing the photographs shown and described in the present paper. A, ultra-violet image; B, fluorescent image; C, approximate image in insect eye.

of organic and inorganic substances. This fluorescence can be easily photographed by placing a second yellow filter (Wratten 2a) between the object and the camera (Fig. 1, B) to absorb the reflected ultra-violet and pass only the visible wave length (λ4000–λ7600) using a panchromatic emulsion for the record. This light is much weaker and requires a far longer exposure than that needed to register the more powerful ultra-violet reflection which must of course be entirely excluded in order that it may not obscure the weaker fluorescence. This fluorescent image is of interest mainly as a comparison between different pigments as it does not enter into the visual picture of any animals under natural conditions.[1]

The fourth photograph is of the greatest interest from the standpoint of insect vision. It is obtained by using the ultra-violet lamp with the No. 18 filter replaced by a blue filter (Jena BG7) in the window of the lamp housing. This illuminates the butterfly with light that includes some ultra-violet but lacks orange and red, a range approximately from λ3300–λ5900 (Fig. 1, C). This is intended to approximate rather closely the visual image in the insect's eye since it includes the photographically very strong ultra-violet band at λ3650. Some of the daylight waves of shorter lengths are excluded by the

[1] Cockayne ('24) has examined a great many butterflies and moths under ultra-violet illumination and recorded the fluorescence observed.

filter glass and optical lenses since the effective lower limit of these is approximately from λ3200–λ3500. As strong invisible light is present, this photographic record can be made only in monochrome since ultra-violet registers as blue in "natural color" transparencies. The use of Kodachrome for this would presumably falsify the image as seen by the insect although we have really not the slightest hint as to what "color" or other impression may result from its proven sensitivity to ultra-violet light. This image may, of course be similar to blue, but there would seem to be absolutely no hope of securing other than metaphysical proof or denial of this.

If we compare the full color transparencies with those made by reflected ultra-violet light, it is at once evident that the patterns are usually changed but to a varying degree that could not be predicted by visual examination. To take, for example, the butterfly and moth, *Papilio laglazei* and *Alcides cydnus* the remarkable similarity of pattern is repeated in ultra-violet, but the moth is only slightly fluorescent. Again, in *Planema aganice* and its supposed mimic *Pseudacraea imitator* the ultra-violet reflection of both butterflies is very similar. Generally in patterns where orange and red predominate, the ultra-violet reflection is reduced, but not so strongly as might be expected, *e. g., Danais plexippus,* but fluorescence is reduced to almost nothing.

In four quite similar but not related species, *Papilio philenor, P. troilus, Argynnis diana* ♀ and *Limenitis astyanax* there are considerable differences in ultra-violet, but much greater ones in fluorescence.

If we examine a dark, brownish-red species like *Danais gilippa berenice* it is seen that there is a strong ultra-violet reflection from the white spots, a weaker, but pronounced one from the red areas and fluorescence is confined to the white spots where it is very brilliant. The photograph including ultra-violet but eliminating orange and red (λ3300–λ5900) has highly corrected color values as judged by the human eye. This is obviously due to the fact that the considerable amount of ultra-violet reflected from the red, combined with some reflection of blue and green compensates for the red and produces an illumination and pattern closely approximating our own impression of this butterfly. That is not an isolated case is shown by similar photographs of *Danais archippus* (Plate 1, figs. 1, 2) (= *Anosia plexippus*). In this species the combination light of λ3300–λ5900 again gives an image well corrected for the human eye. Moreover, in a supposed mimic, *Limenitis archippus,* the same color correction is obtained by these wave lengths (Plate 1, figs. 3, 4) and this correction extends also to a much darker, related butterfly, *Limenitis floridensis* where the red-orange is exceedingly dark (Plate 1, figs. 5, 6).

In other examples of red-orange color the same color relations prevail, as shown by *Danais chrysippus,* var. *alcippus* (Plate 1, figs. 7, 8) and *Hypolimnas doryppoïdes.* These two are also forms regarded as model and mimic respectively.

Another series of models and mimics are represented by heliconiid butterflies and ithomiines of very similar colors and patterns. One or two of these will suffice for our purpose. In *Heliconius eucrate* (Plate 2, figs. 13, 14) and *Mechanites lysimnia* (Plate 2, figs. 15, 16) there is a rather close correspondence of the color pattern in all photographs of each as the pattern is well reproduced, except that the λ3300–λ5900 band gives good differentiation of the orange, which is less clearly marked in the ultra-violet illumination. In *Heliconius eucoma* var. *pardalinus* and *Mechanites agaensis* there is an exception to the general rule as the very deep orange is poorly indicated and the λ3300–λ5900 illumination does not give good differentiation in either species, although the two are essentially similar to one another. In another pair of similarly patterned species, *Heliconius telesiphe* (Plate 2, figs. 9, 10) and a nymphalid, *Colaenis telesiphe* (Plate 2, figs. 11, 12) both the ultra-violet and λ3300–λ5900 range serve to reproduce the pattern very accurately. Comparing *Heliconius melpomene* and the similarly patterned pierid butterfly, *Pereute charops* (Plate 2, figs. 17, 18) it is seen that the λ3300–λ5900 range gives a close similarity, although the ultra-violet alone does not.

As might be expected, species where red or orange do not enter into the pattern the ultra-violet alone gives a closer approximation to the human image than is usually the case where these colors are present. This is seen in two pairs of species, *Amauris niavius* and *Amauris echeria* which are danaines and two varieties of the polymorphic *P. dardanus* (var. *hippocoön* and var. *cenea*). Aside from an excessive reflection from the white and yellow markings, the ultra-violet illumination is a fairly good replica of the human image.

In conclusion it may be repeated that the visual picture of butterflies produced in the human eye differs in varying degrees from photo-

graphs made by reflected ultra-violet light. A range of λ3300–λ5900 which includes some ultra-violet that is photographically very active (λ3650) appears to approach the human image very closely, and theoretically at least should represent the image in the insect eye. It follows that certain red and orange markings are readily visible to insects on account of the ultra-violet that they reflect and not by reason of the reflected orange or red which affects our own eyes.

References

Cockayne, E. A.

1924. The Distribution of Fluorescent Pigments in the Lepidoptera. Trans. Entom. Soc. London, 1924, pp. 1–19.

Eltringham, H.

1919. Butterfly Vision. Trans. Entom. Soc. London, 1919, pp. 1–49, 5 pls.

Luckiesh, M.

1930. Artificial Sunlight. Van Nostrand. New York.

Lutz, F. E.

1933. "Invisible" Colors of Flowers and Butterflies. Journ. American Mus. Nat. Hist., vol. 33, pp. 565–576, 21 figs.

Punnett, R. C.

1915. Mimicry in Butterflies. Cambridge Univ. Press, Cambridge, England.

Radley, J. A. & J. Grant.

1935. Fluorescence Analysis in Ultra-violet Light. Van Nostrand. New York.

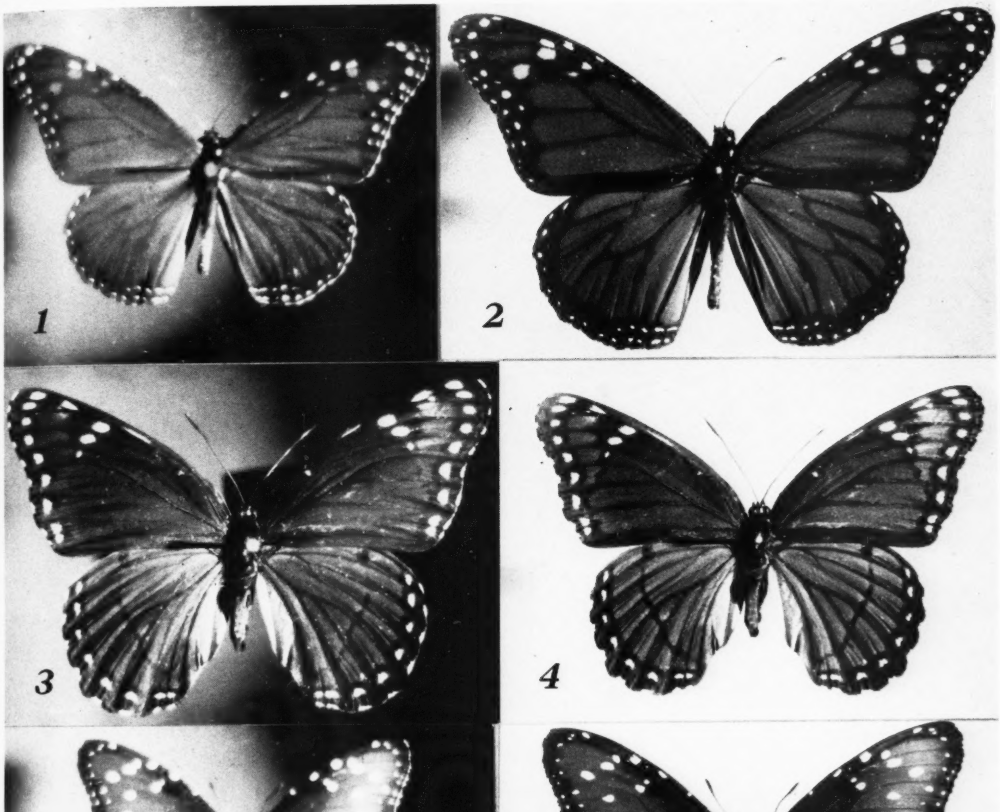
EXPLANATION OF PLATES

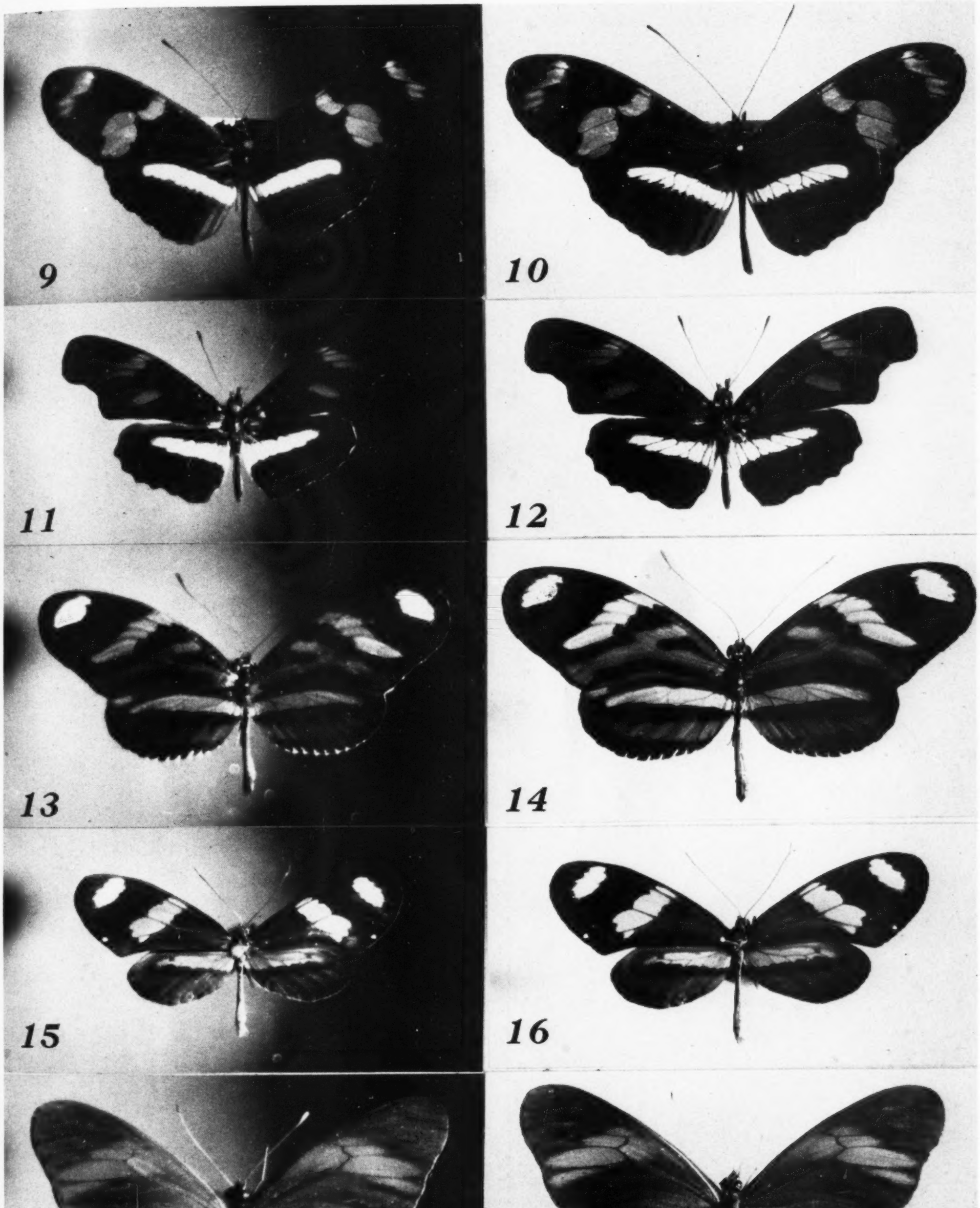
PLATE 1

1. *Danais archippus*, ultra-violet reflection.
2. *Danais archippus*, approximate image in insect eye.
3. *Limenitis archippus*, ultra-violet reflection.
4. *Limenitis archippus*, approximate image in insect eye.
5. *Limenitis floridensis*, ultra-violet reflection.
6. *Limenitis floridensis*, approximate image in insect eye.
7. *Danais chrysippus*, ultra-violet reflection.
8. *Danais chrysippus*, approximate image in insect eye.

PLATE 2

9. *Heliconius telesiphe*, ultra-violet reflection.
10. *Heliconius telesiphe*, approximate image in insect eye.
11. *Colaenis telesiphe*, ultra-violet reflection.
12. *Colaenis telesiphe*, approximate image in insect eye.
13. *Heleconius eucrate*, ultra-violet reflection.
14. *Heliconius eucrate*, approximate image in insect eye.
15. *Mechanites lysimnia*, ultra-violet reflection.
16. *Mechanites lysimnia*, approximate image in insect eye.
17. *Pereute charops*, ultra-violet reflection.
18. *Pereute charops*, approximate image in insect eye.


1
2
3
4
5
6
7
8


9
10
11
12
13
14
15
16
17
18